

DEDUCTIONS ABOUT TRANSSPECIFIC EVOLUTION THROUGH EXTRAPOLATION FROM PROCESSES AT THE POPULATION AND SPECIES LEVEL¹

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ABSTRACT

Information about the basis of transspecific evolution can be obtained only by extrapolation from processes known to take place at subspecific levels. Given sufficient information, such extrapolation is justified by the fact that no processes can be detected at the transspecific level which are different from those that operate at subspecific levels. Nevertheless, certain shifts must be recognized: particularly, greater emphasis on alternative evolutionary strategies, and the greater importance of reproductive as compared to vegetative characters. In addition, the long time span required for transspecific evolution means that many reversals of evolutionary direction can be expected, and common ancestors of modern families and orders are likely to be extinct. Evolutionary conservatism depends upon the complexity of the developmental pattern of a character, and the uniformity versus diversity of the selective pressures to which it might be subjected. Reversibility of evolutionary trends depends upon the number of separate genetic changes needed to produce the change in the original direction. The effect of these deductions on the most widely accepted phylogenetic systems is slight. Principally, weighting of individual characters is regarded as unjustified, linear relationships between modern families are highly unlikely, and cross sectional phylogenetic charts are preferable to the conventional "trees."

At the level of populations and species, the study of evolutionary processes is an exact science. The knowledge which geneticists have now acquired about the extent and organization of hereditary variability in populations, as well as quantitative determinations of the rates at which natural selection can bring about changes, make possible definite predictions which can be tested by means of carefully controlled, quantitative experiments.

This precision, however, is possible only if genetic differences can be estimated by hybridizing different genotypes, and obtaining genetic ratios in the later generation progeny. Consequently, when we are dealing with entities so distantly related to each other that hybridization is either impossible or gives rise only to sterile offspring, the precision of analysis becomes progressively lower. Direct analysis of genetic relationships between genera, families, and other higher taxa is impossible or of only limited application. We can understand evolution at transspecific levels only by extrapolating from results obtained at subspecific levels. Is such extrapolation justified?

THE JUSTIFICATION OF EXTRAPOLATION

Successful extrapolation requires making valid and complete analogies, which are possible only if the proportion of unknown factors is relatively small. For instance, if I knew nothing about the growth of a human child, and should discover that my first born son, originally weighing eight pounds at birth, had

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gained 16 pounds during his first year, I might hypothesize that he would gain twice his starting weight every year, and would weigh 216 pounds at the age of three. Alternatively, I might postulate that he would gain 16 pounds per year throughout childhood, and so would weigh 184 pounds at the age of 11. I would still be wrong, but the absurdity of this conclusion would be less obvious. On the other hand, if I had complete statistics on my own weight and that of my wife during our first ten years, plus similar information on children of relatives who had received nourishment similar to that which I would give to my own son, I could reach a sufficiently accurate estimation of what his weight would be at various ages. In my opinion, the best way of looking at the present symposium is as a major effort to bring together all of the existing knowledge about angiosperm evolution above the species level, and to assess its value in making extrapolations.

We might feel satisfied if our final result is a better description of the course which angiosperm evolution took, as judged from affinities between modern taxa. Nevertheless, we shall fully understand our problem only if our extrapolation can be extended to the formulation of hypotheses about the processes which guided the course of evolution into the numerous and diverse pathways which it has followed. Before we can make this kind of extrapolation, we must first ask ourselves: "are there any processes operating at levels of higher taxa that are unknown at the levels of populations and species." If there are, extrapolations about processes are certainly impossible, and any hypotheses that we might make about phylogeny would be highly suspect.

Fortunately, however, modern molecular biology has effectively disposed of this problem. In addition to mutation, gene recombination, chromosomal repatterning, and natural selection, which are now reasonably well understood at the level of populations and species, two other processes have been postulated by botanists concerned with phylogeny, neither of which can be recognized at the subspecific level. These are (1) "macromutations," which could at one step give rise to a population belonging to a new genus, family, or order; and (2) "orthogenesis," by means of which evolutionary direction is believed to be determined not by interactions between populations and their environment, but by directed mutations occurring within the genotype, unaffected by the environment.

The implausibility of both of these hypotheses has long been recognized by evolutionary geneticists (Fisher, 1930; Dobzhansky, 1941), as well as by paleontologists who are familiar with the genetic facts (Simpson, 1953). Their virtual impossibility is dictated by the complex relationships now known to exist between genes and characters (Watson, 1970; Monod, 1971). A single gene can provide information for only one polypeptide chain. Its primary product may be a monomer enzyme, capable of catalyzing a single step in a complex biosynthetic pathway. More often in higher organisms, the polypeptide chain is part of a multimer enzyme, of a complex supra-molecular architecture of structural protein or a unit in the system of regulators that we must postulate in order to understand gene action in multicellular organisms (Britten & Davidson, 1969, 1971). Single gene mutations, therefore, can never do more than alter a single, small part of a complex, highly coordinated developmental system. If the alteration is profound, the phenotype may deviate greatly from normal, but since the harmony of

development has been violently disturbed, this mutant phenotype will always be an inadaptive monster. Major changes, such as those responsible for new genera, always take place by the accumulation of scores or hundreds of genetic differences, most of which, individually, have only small effects on the phenotype.

Orthogenetic trends, determined by mutation alone, would require that large numbers of diverse genetic changes be somehow coordinated to produce a phenotypic effect entirely different from that which one or a few of them could produce by themselves. At the gene level, the kind of mutation needed to alter one kind of structural or control protein in a direction that would favor, for instance, the "fusion" of petals would be entirely different from the kind of mutation which in another protein would contribute toward the same result. Coordination of these diverse changes is conceivable only via the action of natural selection.

This does not mean, however, that trends of evolution are governed solely by random mutations exposed independently and separately to the selective action of the external environment. Geneticists now recognize that the adaptive value of a mutation may depend as much or more upon the other genes with which it is associated in an individual genotype as upon its own interaction with the environment. The pre-existing genotype has a powerful screening effect on new mutations, which becomes ever more stringent as adult structures and their developmental pathways become more complex. If a particular evolutionary line has already evolved a radially symmetrical corolla having a short tube, mutations promoting a longer tube will be favored, while those promoting the shift to bilateral symmetry are less likely to become established. If, on the other hand, evolution toward a choripetalous, zygomorphic corolla has begun, mutations toward sympetaly are likely to be rejected and those leading toward zygomorphy tend to be favored. The consequences of this difference are explored below.

A second question which must be satisfactorily answered before we can justify extrapolation from the subspecific to the transspecific level is: are there any morphological characteristics that play major roles in the origin of genera and families, but which never appear as differences between species of the same genus? After carefully reviewing this subject, I have become convinced that there are no such characters. Even differences which are regarded as "most fundamental," such as that between hypogyny, perigyny, and epigyny, exist at the level of species differentiation in genera such as *Saxifraga*. The "fundamental" difference between monocotyledonous, dicotyledonous, and tri- or tetracotyledonous embryos and seedlings separate different species or species groups in genera such as *Pittosporum*, *Ranunculus*, and others (Stebbins, 1974).

SHIFTS OF EMPHASIS BETWEEN SUBSPECIFIC AND TRANSSPECIFIC LEVELS

Nevertheless, the action of the evolutionary processes and the characters that they alter are different at transspecific levels from those prevalent at subspecific levels. The difference, however, is one of emphasis rather than kind. With respect to characters, a well known fact is that reproductive structures are increasingly valuable at higher levels, as compared to vegetative characters. This trend, however, is no more than a moderately high correlation, and many exceptions

exist. Vegetative characters such as cotyledon number, seedling development, wood structure, and presence versus absence of stipules are, as a rule, more important at higher than at lower levels of the taxonomic hierarchy. Among reproductive characters, those of the gynoecium are more often significant at the level of genera and families than those of the androecium and floral envelopes. The reasons for this difference are discussed later.

With respect to evolutionary processes, one phenomenon which becomes increasingly significant at higher taxonomic levels is that of alternative evolutionary strategies. For instance, the adaptive shift in flowers from insect to bird pollination must involve the appearance of a long, narrow tube which fits the bird's beak, and contains nectar at the bottom. This structure can be evolved by means of lengthening and straightening the spur on a sepal (*Delphinium*) or a petal (*Aquilegia*); by evolving a long, narrow corolla tube (*Kniphofia*, *Pentstemon centranthifolius*), or a hypanthium (*Zauschneria*, *Fuchsia*); or by evolving a corolla in which the lower parts of separate petals are much elongated and overlap each other (*Erythrina*). Response to selection for higher seed production in an evolutionary line that is occupying a progressively more favorable climatic zone can be accomplished by increasing the number of ovules per carpel, carpels per flower, flowers per inflorescence, or inflorescences per plant. Increased efficiency of seed dispersal by either wind or animals can be evolved via modifications of seeds, segments of fruits, entire fruits, fruits plus calyces, or entire inflorescences (Stebbins, 1970b, 1971, 1974). Phylogenetic trends are often determined not by the particular kind of selective pressure which is operating, but by the way in which the population or evolutionary line responds to a generalized kind of selective pressure.

Given the possibility of alternative evolutionary strategies, what determines the particular strategy which a given evolutionary line will adopt? This is determined chiefly on the basis of evolutionary canalization, a principle which states that evolutionary lines tend to follow certain pathways, the nature of which is governed by two principles: conservation of organization and adaptive modification along the lines of least resistance. These principles can be stated as follows.

Conservation of organization means that if a structure has evolved which requires for its development a complex, highly coordinated sequence of gene actions, it tends to be preserved and modified as evolutionary lines become adapted to new conditions. Even if an entirely new structure would produce a better adaptation, the complex "genetic revolution" that is required to produce it is very unlikely to take place, particularly if one part of this "revolution" involves an inadapative intermediate stage.

Adaptive modification along the lines of least resistance means that evolutionary lines usually become adapted to new conditions by whatever changes involve the smallest number of gene substitutions. In angiosperms, these most often are quantitative alterations of the amount or the duration of activity of a particular kind of undifferentiated meristem.

The operation of these principles to determine which evolutionary strategy will be adopted in the shift to bird pollination is as follows. In *Delphinium* and *Aquilegia*, which have, respectively, spurred sepals and petals in those ancestral

species that are adapted to bee pollination, modification of these spurs is the path of least resistance. In *Pentstemon*, on the other hand, the ancestral bee pollinated species already possessed a corolla tube, the modification of which for bird pollination required relatively little adjustment of the gene-controlled developmental pattern. The Onagraceae, on the other hand, have separate petals and so lack a corolla tube, but usually have a more or less well developed hypanthium, the modification of which into a floral tube adapted to the bird's beak was the path of least resistance in the evolutionary lines leading to *Zauschneria* and *Fuchsia*. The role of evolutionary canalization in determining evolutionary strategies with respect to mechanisms for seed production and dispersal has been discussed elsewhere (Stebbins, 1967, 1970b, 1971, 1974).

These examples all illustrate a cardinal principle which operates generally at the transspecific level, but which is much less likely to be evident at the level of populations and closely related species. Given an initial diversity with respect to certain adaptive structures, response to the same kind of selective pressure is just as likely to promote their divergence via the adaptation of different kinds of responses to this pressure, as to promote parallelism or convergence. In other words, whether two independent evolutionary lines will diverge, evolve parallel to each other, or converge depends both upon the similarity or difference between the kinds of selective pressures to which they are subjected, and the nature of preexisting structures which might be modified in response to these pressures.

Another factor that is of primary importance in evolution at transspecific levels is the long time span that is necessarily involved. Species can often be differentiated in as short an interval as two to a hundred generations (Grant, 1971). On the other hand, no valid genus of angiosperms known to me can be clearly shown to be less than five million years old (Pliocene), and most of them are much older. The effect of this time span is twofold. In the first place, the evolutionary history of most plant genera covers time spans during which both the earth's climate as a whole and that of local regions has oscillated from favorable to unfavorable conditions, and back again. This means that many opportunities have been available for evolutionary lines to reverse their direction of adaptational change. Such reversals have been commonplace. An example in the subtribe Microseridinae of the Cichorieae, Compositae, is discussed elsewhere (Stebbins, 1972a). I believe that whenever two groups of angiosperms exist sympatrically, and differ with respect to the advancement, specialization, or efficiency of their reproductive structure, careful analysis will show that the more advanced group has not evolved from the less advanced group in situ, but by an indirect route, involving first adaptation to different, usually more severe conditions, followed by later readaptation to the conditions that make possible the sympatry.

Another effect of long time spans is extinction. Comparisons between families having well defined genera and those in which generic lines are blurred show clearly that the distinctness of genera depends largely upon extinction of species intermediate between them and other genera (Stebbins, 1956). This extinction is most likely to effect the immediate ancestors or the earliest representatives of any highly successful group, since these forms are the most likely to come into direct competition with members of the successful group. This fact is largely

responsible for a phenomenon of primary importance in constructing phylogenetic trees. No modern, successful group, including the angiosperms themselves and the two major subdivisions of the class, Dicotyledons and Monocotyledons, can be regarded as a descendant of any other living group. Even the use of the suffix "-like" to indicate that a hypothetical ancestor was so much like some living group that, had botanists been present when it lived they would have been able to classify it in that group, is inadmissible. This contention is supported by fossil evidence whenever it is available. The seed plants which have the best fossil record are the conifers. In them, Florin (1951) has shown clearly that the common ancestors of the principal modern families, Pinaceae, Taxodiaceae, Cupressaceae, Taxaceae, and Podocarpaceae, are so different from any modern group that they could not possibly be reconstructed except on the basis of fossils. The same is true of animals generally, particularly vertebrates (Romer, 1966). There is no reason to believe that the situation in angiosperms is any different. Bailey & Nast (1945) already emphasized the profound differences that exist between all of the presumably primitive groups that are placed in the woody Ranales or Magnoliidae of Cronquist. Moreover, every one of these groups is highly specialized in at least one or two characteristics. Consequently, in the absence of significant fossils, so many unknown factors exist that the method of extrapolation is inadequate as a means of deducing what ancestral forms were like on the basis of the morphology of any living angiosperms. Such extrapolation can be very misleading.

INTERPRETATIONS OF PHYLOGENETIC TRENDS ON THE BASIS OF EXTRAPOLATION

Even though, as has just been mentioned, the method of extrapolation is inadequate to determine actual phylogenetic relationships, except at the level of recently evolved genera within a family, it can provide valuable evidence about the general nature of phylogenetic trends, and the conditions that would be favorable to a particular kind of morphological change. In the remainder of this article, extrapolation will be used to suggest interpretations of this nature.

THE TAXONOMIC SIGNIFICANCE AND DEVELOPMENTAL-GENETIC BASIS OF EVOLUTIONARY CONSERVATISM

Characters that are valuable at the level of genera and families must have a moderate but not extreme degree of conservatism. Characters having extreme genetic plasticity, such as the size, shape, and texture of leaves, are rarely of value at these levels. On the other hand, the more conservative characters, such as roots, phyllotactic arrangements of leaves, numbers of floral whorls, ovule structure, and the nature of the embryo sac, are useful only in a relatively small proportion of groups within which they show significant variation. Characters having intermediate degrees of conservatism can either be very valuable or valueless, depending upon the group. For instance, characters of the corolla and androecium are of relatively little value in separating genera of Rosaceae, are valuable in Leguminosae chiefly at the level of subfamilies or tribes, and in Primulaceae, Scrophulariaceae, Labiatae, and other sympetalous families are among the most important characters for defining genera. On the other

hand, characters of the gynoecium are relatively important in Rosaceae and Leguminosae, but much less important in Primulaceae, Scrophulariaceae, and Labiatae. Is the degree of conservatism of a particular character within a group a purely chance affair, or it is related to factors that might be analyzed as a means of determining its adaptive basis, if any?

I would like to suggest that the degree of conservatism of a character is related to two factors: the complexity of its developmental pattern and the diversity of selective pressures to which it might be subjected. Leaves, for instance, have a relatively simple developmental pattern. If they are subjected to similar selective pressures during a long period of evolution, as is true of the leaves of most Lauraceae and Orchidaceae that inhabit tropical forests, they are too conservative to be of any taxonomic value. On the other hand, if they are subjected to highly diverse selective pressures, as in the herbaceous Rosaceae of temperate regions, they are so variable that they can serve only to distinguish closely related species and subspecies. In the Umbelliferae, the perianth has a simple developmental pattern, and is of little taxonomic value; in most sympetalous groups, particularly those that are zygomorphic, the developmental pattern of the corolla is highly complex, and it usually is sufficiently variable that its variations are of great taxonomic value. In groups having relatively small and simple corollas, which are pollinated by a variety of relatively unspecialized insects, differences in the corolla are most valuable at the level of genera. In groups having larger corollas, and pollinated by more specialized insects, or by special methods such as pseudocopulation, differences between corollas are most valuable at the level of different species within a genus.

In general, characters of the gynoecium are more likely to be significant at the level of families than are those of the androecium. I believe that this tendency toward greater conservatism of gynoecial characters is based upon two facts. In the first place gynoecia are compound structures, the parts of which (ovary wall, style, stigma, and ovules) differ greatly from each other in adaptive function. Their developmental pattern is, therefore, usually more complex than that of the corolla. Secondly, the selective pressures to which they are subjected depend more upon integration of diverse functions than upon adaptation of individual functions to specific alterations of the environment. The receptive surface of the stigma, for instance, must be adjusted to the external structure of the pollen grains, while the length of the style must be in harmony with the amount of food reserves which pollen grains possess. With respect to ovules and seeds, adaptation depends upon a number of factors that in some ways conflict with each other (Stebbins, 1971): seed size, nature of dispersal mechanisms, length of seed development period, and vigor of seedlings. The adaptive balance that any species has acquired can be altered only by coordinated changes with respect to several of these characters.

REVERSIBILITY VERSUS IRREVERSIBILITY OF EVOLUTIONARY TRENDS

As has been clearly stated by Simpson (1953: 310–311), Dollo's law of irreversibility cannot be applied to single characteristics that have a simple genetic basis. It is valid only if a particular kind of evolutionary change involves

coordinated alteration of many different characteristics, or of a single characteristic which has a highly complex developmental pattern. If one or both of the latter situations exist, the result of evolutionary canalization will be the tendency of a structure to evolve in a new direction in response to a reversal of selective pressure, rather than a return to the original state. Abundant examples of secondary reversal from wind to insect pollination exist throughout the angiosperms, but the revertants are always completely different in structural characteristics from primitively insect pollinated species (Stebbins, 1970a). A good example is the genus *Ficus* and others of the Moraceae. Secondarily derived shrubs, such as various Chenopodiaceae, Nyctaginaceae, and the genus *Artemisia* of the Compositae, are completely different in stem anatomy from primitively woody species (Stebbins, 1972b). In the Cichorieae, the genus *Tragopogon*, a mesophyte which has probably been derived secondarily from more xeric ancestors, has leaves entirely different from those possessed by primitively mesic Cichorieae (Stebbins, 1952).

With respect to single characters such as numbers of similar parts, these are determined largely by the amount of undifferentiated meristem available at the time when a particular kind of organ is being differentiated, or the length of time over which a shoot apex will possess a meristem having a particular kind of developmental potential (Stebbins, 1967). Since these developmental events are simple and quantitative, they are subject to genetically determined alterations in either direction, and hence to reversal. With respect to the number of serially produced parts, such as leaflets of a compound leaf, flowers of an inflorescence, sepals, petals, stamens and carpels or ovary locules in a flower, or ovules per locule, taxonomists in the past have tended to read the series in only one direction, usually from many to fewer parts. After considering carefully many such series, I am convinced that in the vast majority of them the true directions have been those that one would expect on the basis of adaptive radiation; from some point in the middle of the series toward an increase in some derivative lines, and a decrease in others.

Other single character differences, such as "fusion" of sepals or petals, as well as the trend from hypogyny to perigyny and epigyny, are based upon differences with respect to a complex developmental pattern, involving the initiation of an intercalary meristem at a precisely regulated stage of development, and its cessation at an equally precise stage. From the point of view of developmental genetics, such differences are comparable to differences with respect to many separate morphological characteristics, since alterations of several separately acting genes are involved. Reversal of such trends can be expected only rarely or not at all.

BEARING OF THESE DEDUCTIONS ON THE NATURE OF PHYLOGENETIC SYSTEMS

If taxonomists take into account the principles and deductions which I have discussed, they will not need to alter very much the phylogenetic schemes that have been proposed more recently for the Angiosperms, particularly those of Takhtajan (1966, 1969) and Cronquist (1968). The concept of alternative evolutionary strategies predicts that certain kinds of major alterations of the flower,

such as the origin of sympetaly, epigyny, and the herbaceous growth habit will be repeated independently in many different groups, so that similarity with respect to such characters is not by itself evidence of relationship. The principal differences between the Cronquist-Takhtajan system and the older ones that resemble it are of this nature. The extrapolation of the concept of adaptive radiation to transspecific levels predicts that modern families can rarely be arranged in a linear series from most primitive to most advanced: the evolutionary "tree" is actually a much branched shrub. This form is characteristic of the Cronquist-Takhtajan system.

Two of the conclusions reached here do affect the nature of the Cronquist-Takhtajan system to some extent. First, because of the complex relationships between changes at the gene level and the alteration of morphological characters, as well as the importance of preexisting characters in determining the direction of evolution, the weighting of individual characters which regards some as of critical importance in determining the phylogenetic position of a group, and others as much less important, is unwarranted, at least in our present state of knowledge (Stebbins, 1974). Second, the high probability that the common ancestor of any two modern families or orders is extinct, and cannot be reconstructed by extrapolation from modern forms means that all phylogenetic trees are suspect. Much more realistic are cross sectional diagrams, such as those of Rodriguez (1956) and others which show relationships between modern groups without specifying the precise evolutionary pathways by which they arose. Phylogenetic primitiveness or advancement can be expressed by placing the orders at varying distances from a central point, which expresses in a very general way the characters of a hypothetical common ancestor, without attempting to describe or name it. This is, admittedly, not very satisfying for those taxonomists who wish to believe that we understand the directions of angiosperm evolution. Nevertheless, it is realistic: the unpleasant but inescapable fact is that, lacking an adequate fossil record, the evolutionary relationships between modern subclasses and orders of Angiosperms may never be fully understood. Our systems must reflect our ignorance as well as our knowledge.

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